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THE IDENTIFICATION OF LARVAL *PARASUDIS* (TELEOSTEI, CHLOROPHTHALMIDAE); WITH NOTES ON THE ANATOMY AND RELATIONSHIPS OF AULOPIFORM FISHES

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Abstract. Larvae and transforming individuals of *Parasudis* are identified and described for the first time. The phylogenetic integrity of the family Chlorophthalmidae is investigated and restricted to the sistergenera, *Parasudis* and *Chlorophthalmus.* Two derived morphological characters support the monophyly of an extended Ipnopidae which now includes the genus *Bathysauropsis.* The "rostral cartilages" in aulopiform fishes are reviewed and the homology of these and associated structures throughout the lower Neoteleostei is questioned.

INTRODUCTION

Parasudis truculenta (Goode and Bean, 1895) is a relatively common offshore fish found from off northern New England to equatorial Brazil. Adult specimens have been taken only in bottom trawls at depths of ca. 180 to 480 m, but dietary studies suggest that *Parasudis* moves off the bottom to feed in midwater (Mead 1966). The species is hermaphroditic, and ripe specimens have been collected from February to May (Mead 1960). Neither the eggs nor the larvae of this species have yet been described (Okiyama 1984).

The purpose of this paper is to describe larval and transforming *Parasudis,* and to comment on aspects of anatomy and relationships. There is considerable confusion in current literature regarding

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the systematics and classification of Rosen's (1973) Aulopiformes (see Johnson 1982; Okiyama 1984; Rosen 1985; Stiassny 1986). The resolution of this problem is beyond the scope of this paper and for the purpose of this study we adhere to Rosen's classification of the Order (1973:509).

MATERIALS AND METHODS

Specimens are from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology, Harvard University (MCZ); the Atlantic Research Centre, New Brunswick (ARC); the DANA collections of the Zoological Museum, University of Copenhagen (ZMUC); the National Museum of Natural History, Washington, D.C. (USNM); the British Museum of Natural History (BMNH) and the University of Miami (UMML). The specimens used in this study are listed in appendix under material examined.

Counts and measurements follow Hubbs and Lagler (1964). For osteological examination, selected specimens were cleared and stained following the procedure of Dingerkus and Uhler (1977); these specimens are indicated "c.s." under material examined. Anatomical drawings were made with the aid of a Zeiss SV-8 stereomicroscope with a camera lucida attachment. Osteological and syndesmological nomenclature follows Stiassny (1986).

DIAGNOSIS

Parasudis larvae are characterized by the distinctive bulbous shape of the snout, the pattern of snout, opercular and caudal pigmentation, as well as by a particular basihyal form and dentition. The larvae are further distinguished from those of other chlorophthalmoid taxa by having 38 to 39 vertebrae and/or myomeres (Okiyama 1984:208).

DESCRIPTION

Larvae
(Figs. 1A, B and C)

Preflexion or flexion larvae are not present among the material examined, and the following description is based on 85 postflexion

specimens ranging from 10.6 to 80 mm standard length (SL). Specimens of 15.4 and 30.6 mm SL are illustrated in Figs. 1A–C. The body is elongate, oval to round in cross section at maximum depth; maximum depth 6.4 to 9.4 times in SL; maximum body width subequal or equal to maximum body depth (7.8 to 11.7 in SL). Head length (HL) 2.6 to 3.9 times in SL, probably negatively allometric. Bulbous snout rounded in anterodorsal profile, 2.2 to 3.0 times in HL. Eyes large, 3.5 to 5.0 times in HL. The eyes often appear stalked or partially stalked (Fig. 1B). The presence (or absence) of stalked eyes may be a result of damage incurred during collection; however, stalked and non-stalked specimens do appear in the same samples. The eyes of both larval and transforming individuals lack the "keyhole" shaped aphakic space characteristic of adult chlorophthalmids.

All larvae examined appear to have a full complement of fin elements, although, the fragile fin rays are often damaged. The origin of the dorsal fin (10 rays) is slightly posterior to the base of the pectoral fin (17 rays). The narrow-based adipose fin is positioned above the second or third anal ray (8–9 anal rays). The pectorals are at mid-body level with their bases almost under the thin opercular flap. Pelvic fin (9 rays) origin is below the anterior half of the dorsal fin. The caudal fin is forked even in the smallest specimens. Procurrent caudal rays are present and increase in number with growth. The anus is located well caudad of the pelvic fin base but closer to the insertion of the pelvic than to the insertion of the anal fin.

The dentition remains relatively constant throughout the larval period. Both the premaxillae and the dentaries bear single rows of evenly spaced caniniform teeth (Fig. 2). Anteriorly, these larval teeth are recurved, but are markedly retrose in the posterior aspect of both upper and lower jaws. Two to three small recurved caniniform teeth are implanted along the anteriolateral aspect of the dentary (Fig. 2).

In most specimens a few small caniniform teeth are inserted along the body of the palatine cartilages, and in the ventral hypobranchial apparatus a markedly elongate basihyal cartilage bears small recurved fang-like teeth on its anterior margin (Fig. 3A).

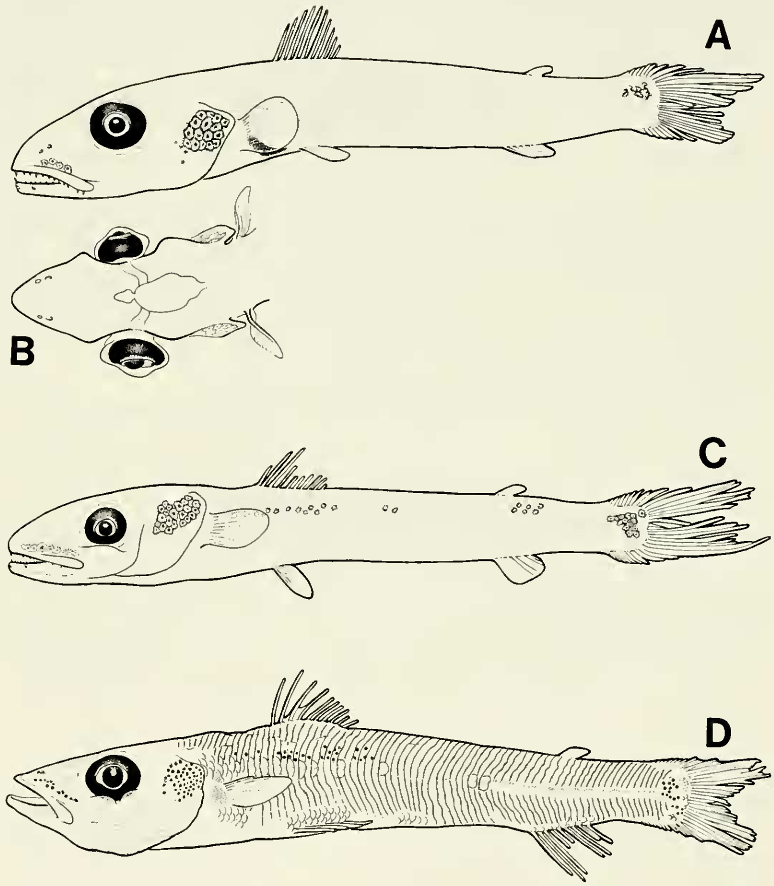

Figure 1. *Parasudis truculenta.* (A) Lateral view of larva 15.4 mm SL (MCZ 62400). (B) Dorsal view of head of same specimen. (C) Lateral view of larva 30.6 mm SL (MCZ 62399). (D) Lateral view of transforming juvenile 85 mm SL (MCZ 62401). Note that the dotted lines on the body in (A) and (C) represent myosepta while the solid lines in (D) represent the pigmented edges of scale pockets. Drawn by S. Landry.

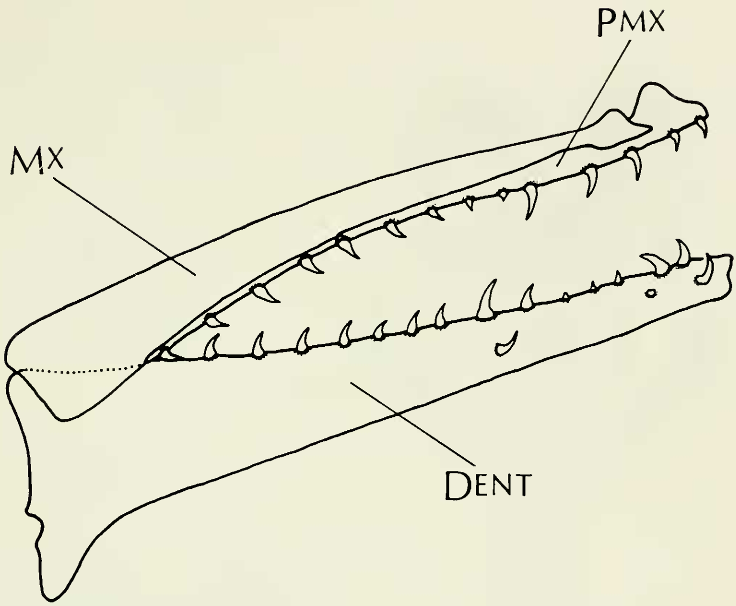

Figure 2. Isolated buccal jaws of larval *Parasudis* (MCZ 62397, 38 mm SL).

Abbreviations: Dent, dentary; Mx, maxilla; Pmx, premaxilla.

Pigmentation

Body color in preserved specimens is a uniform opaque white although very infrequently a light tan or brown wash is present. Live coloration is unknown, but based on observations of live pretransformation *Chlorophthalmus* (Hartel personal observation), living *Parasudis* larvae are presumed to be almost translucent in seawater.

Opercular pigmentation covers an area almost as large as that of the eye and at times may be quite dark. Opercular pigmentation is present in the smallest specimen examined.

Initially, a small group of melanophores is situated on the caudal peduncle above the midline. With growth (>30 mm SL) the pigmented area becomes roughly triangular in outline with the posterior lower corner extending below the midline (Fig. 1C). A melanophore distinct from the triangular patch and situated in the upper corner of the caudal base is found in specimens greater than 22 mm

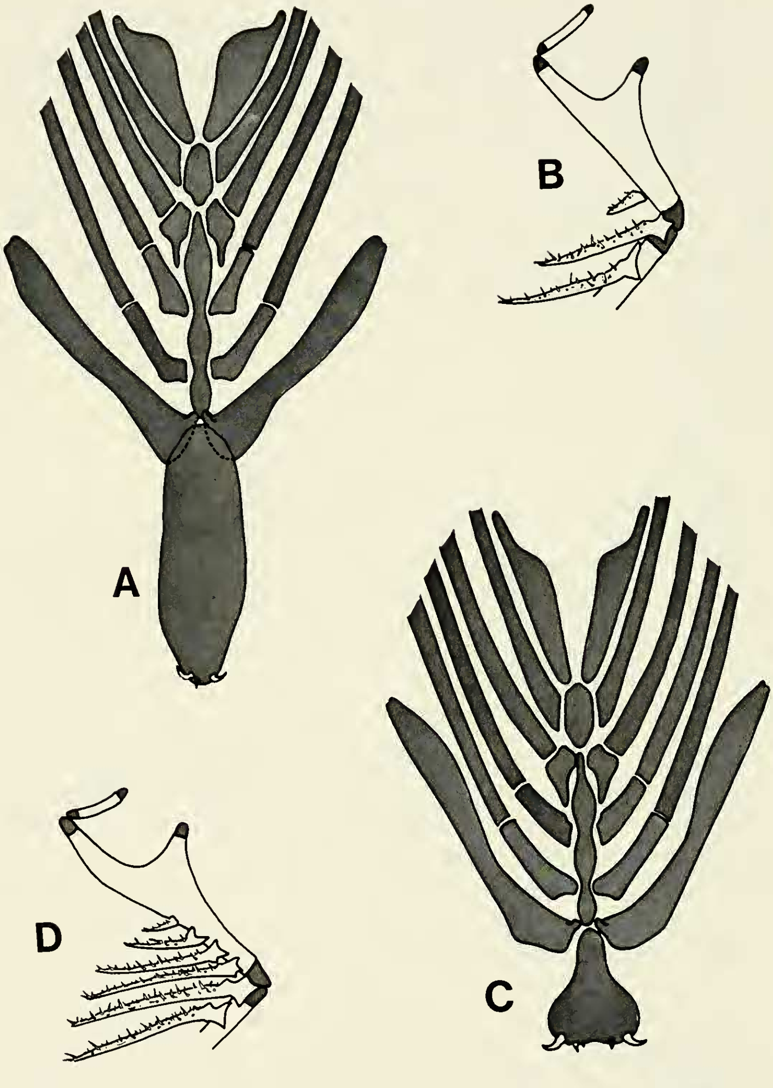

Figure 3. *Parasudis.* (A) Ventral gill arch elements and hyoid apparatus of larva 30 mm SL (MCZ 62398). (B) First epibranchial and associated structures of adult specimen (MCZ 40561). *Chlorophthalmus.* (C) Ventral gill arch elements of larva 22 mm SL (MCZ 62403). (D) First epibranchial and associated structures of adult specimen (MCZ 40509).

SL, and a second is usually developed at the lower corner of the caudal base by 30 mm SL.

Pigmentation in the snout region first appears as a single melanophore above the anterior end of the maxilla at 14 mm SL. Additional melanophores are added posteriorly in a line just above the maxilla and by 50 mm SL, the row reaches a point almost under the anterior margin of the orbit.

Lateral body pigmentation begins as one or two mid-body melanophores at 22 mm SL. The melanophores increase laterally in two groups. Four are present under the dorsal, and three are under the adipose fin by 24 mm SL. At 40 mm SL the melanophores, which are always found directly over a myomere, form an almost continuous band. There are one, two or sometimes three melanophores per myomere.

Deep pigment is present in the dorsal midline as a small dark spot just posterior to the dorsal fin. Ventrally a similar small midline spot is found at mid-body. An additional line of deep pigment is present along the midventral caudal peduncle. All of these deeper markings become less noticeable with growth as the muscle tissues become denser. Internal pigment is often visible through the bodywall below the base of the pectoral fin (Fig. 1A). This darkened area is densely pigmented mesentery supporting the viscera and areas of visceral peritoneum wrapping partially around the developing anterior viscera. The pigmented mesentary extends caudad almost to the level of the anal fin origin (Fig. 4).

Transforming specimens
(Fig. 1D)

This description is based upon two specimens, 75.5 mm SL (MCZ 57922) and 85 mm SL (MCZ 62401), illustrated in Fig. 1D. The larger specimen is only 5 mm larger than the largest available larval specimen (ARC 6879), yet marked morphological changes are evident.

General body proportions remain constant, but the form of the head is altered by the loss (via reabsorption?) of the characteristic bulbous larval snout. The smaller individual retains a few of the larval retrose jaw teeth and has a strong basihyal dentition. In the larger transforming fish the jaws are edentulate, apparently having lost the larval teeth and not yet having developed the juvenile/adult

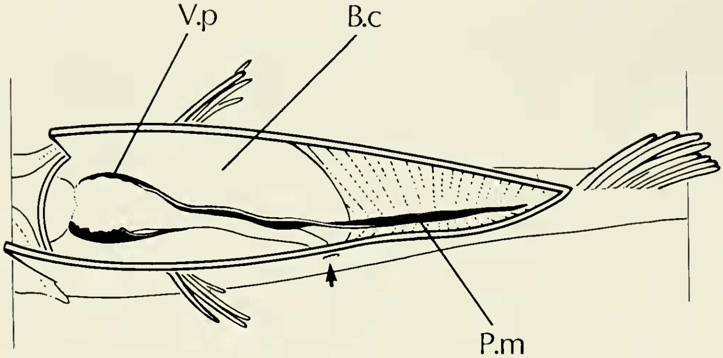

Figure 4. Internal pigmentation of larval *Parasudis* (based on two specimens; MCZ 63055, 40 mm SL and MCZ 63056, 31 mm SL). Drawn by S. Landry.

Abbreviations: B.c, body cavity; P.m, pigmented mesentery; V.p, visceral peritoneum.

dentition. A few small palatine teeth are present, and small teeth are embedded in the dermis overlying the basihyal element. As the smaller of the two transforming specimens is badly damaged and contorted, the remaining description is based solely upon the 85 mm SL specimen.

The diagnostic larval pigmentation pattern is faint but the remnants of snout, opercular, lateral and caudal pigmentation are still discernible. Patches of scales are present and, as is indicated in Fig. 1D, these have a distinctive pattern of implantation. Each scale pocket is located on a continuous flap of skin which is strongly pigmented along its distal margin. The resultant "herringbone" pattern is clearly visible in adult specimens (Mead 1966: Fig. 47) and where scales have been lost, corresponds to approximately two pigment lines per scale.

Transformation apparently occurs rapidly. We have seen a fully transformed juvenile (MCZ 41840) the same length as the larger transforming larva. The fully transformed fish has the definitive adult dentition (see Mead 1966), is scaled, and has lost almost all traces of larval pigmentation. During transformation the snout becomes increasingly flattened and "shrunken," lending the fish its characteristic "duckbilled" appearance. Apparently, a loss (reabsorption?) of the somewhat gelatinous larval body tissues results in a

more attenuated body form in the recently transformed juvenile. Halliday (1968: Fig. 1) illustrates a 99.0 mm SL transformed juvenile that shows initial body deepening.

The internal pigmentation of the anterior viscera is present in transforming specimens. Apparently during transformation, pigment migrates from the visceral peritoneum onto the parietal peritoneum, and the pigmentation of the caudad extension of the mesentery is greatly reduced. In fully transformed juveniles the parietal peritoneum is strongly pigmented throughout the abdominal cavity but little pigment is associated with the visceral peritoneum.

We have examined a number of transforming *Chlorophthalmus* specimens from both the North Atlantic Ocean and the Coral Sea. In each of these specimens, tranformation occurs at a considerably smaller size (ca. 35 to 40 mm SL) than that observed in our *Parasudis* specimens.

DISTRIBUTION

The western Atlantic specimens we have examined come from areas off the Brazilian coast to areas east of the southern tip of Nova Scotia (Fig. 5). Included in our study is one eastern Atlantic specimen (MCZ 62402). Preliminary morphometric analysis of this larva and its eastern Atlantic locality indicate that it may represent *Parasudis fraser-brunneri* (Poll 1953). However, due to a lack of additional material for detailed study and the close morphological resemblance of *P. fraser-brunneri* to *P. truculenta* (see Mead 1966:184), we are unable to confirm the specific identity of the eastern Atlantic specimen.

All of the larval *Parasudis* were taken in midwater trawls. Specimens from the WHOI opening and closing nets (MOC 10 and 20) indicate that the larvae are most commonly taken above 150 m (five collections: 70 to 0 m; 0 to 100 m; 70 to 140m; 0 to 203 m; 70 to 150 m). Information from non-closing nets indicate similar distributions. However, other collections taken with non-closing nets indicate that the larvae may approach the surface rather closely, since *Parasudis* larvae are found in collections taken above 50 m. Except for a few larvae from the relatively shallow Straits of Florida, all specimens were taken in trawls over ocean bottoms from 1937 to 4934 m deep.

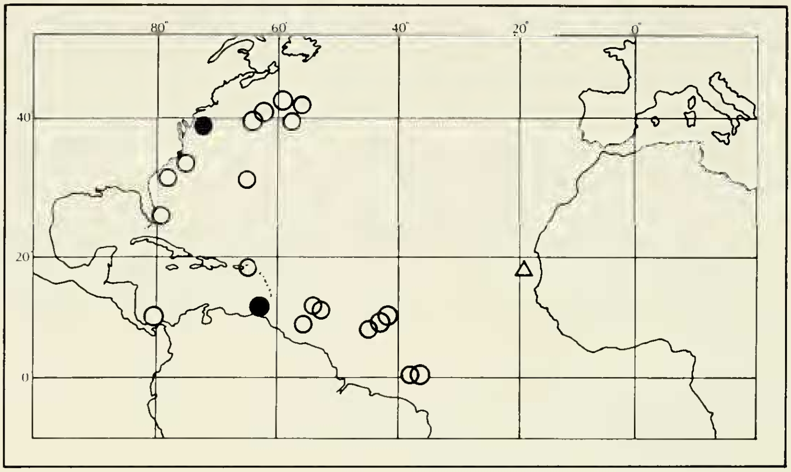

Figure 5. Distribution of larval *Parasudis* examined during this study. Open circles: *P.truculenta*. Solid circles: transforming larvae. Triangle: *P.?fraser-brunneri* larva (MCZ 62402). Symbols may represent more than one sample.

GENERIC PLACEMENT

As currently constituted the family Chlorophthalmidae (=Chlorophthalminae of Sulak 1977 and Nelson 1984) comprises three genera of benthic fishes (Okiyama 1984): *Chlorophthalmus* Bonaparte, 1840 (18+ species), *Parasudis* Regan, 1911 (two species) and *Bathysauropsis* Regan, 1911 (three species). Representatives of the former two genera inhabit the North Atlantic; *Bathysauropsis* is known only from the deep waters (2000 to 2500 m) of the South Atlantic and South Pacific (Mead 1966).

Based on adult morphology, Mead (1966) presented a key to chlorophthalmid genera; we note that *Parasudis* is further distinguished from the other two genera by having a single gill raker along the anterior border of the first epibranchial (Fig. 3B). In both *Chlorophthalmus* (Fig. 3D) and *Bathysauropsis*, the first epibranchial bears at least two or more lath-like denticulate gill rakers along its anterior margin.

Predorsal number distinguishes the three genera. Adult and larval *Parasudis* have a single predorsal bone (Figs. 6A, B). *Chlorophythalmus* have two (Figs. 6C, D), adult *Bathysauropsis* have three.

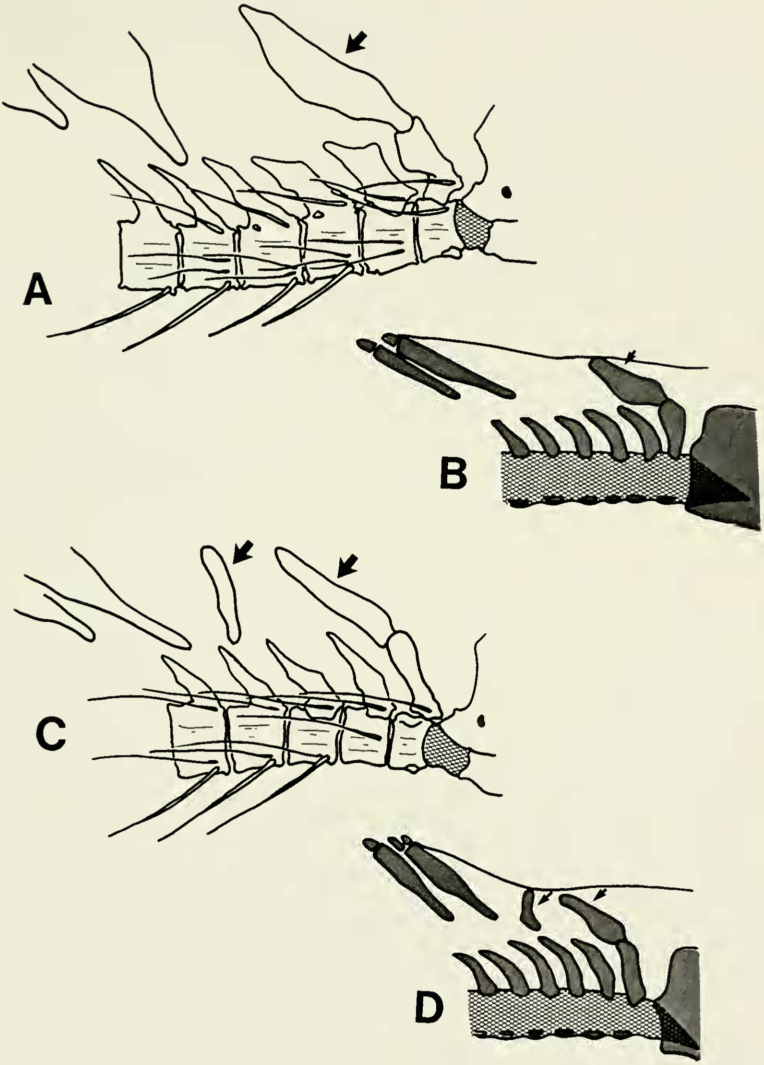

Figure 6. *Parasudis.* (A) Posterior region of the neurocranium, vertebral column and predorsal bones of adult specimen (MCZ 40561). (B) Larva 30 mm SL (MCZ 62398). *Chlorophthalmus.* (C) Posterior region of the neurocranium, vertebral column and predorsal bones of adult specimen (MCZ 41444). (D) Larva 22 mm SL (MCZ 62403). Arrows indicate predorsal bones.

Johnson (1982) discussed predorsal (=supraneural) number among aulopiforms and noted a trend towards predorsal reduction throughout the assemblage. He cited notosudids (=scopelosaurids) and *Omosudis* as other taxa with a single predorsal. Sulak (1977) stated that ipnopine genera bear one of two predorsals.

The anal position and lack of anal pigmentation during transformation of *Parasudis* contrasts with that of *Chlorophthalmus* where the anus is situated closer to the pelvic base (see Mead 1966), and is highly pigmented during transformation. Other pigment characters of the anterior visceral cavity separate *Parasudis* and *Chlorophthalmus.* In *Parasudis* the larval pigmentation is confined to the visceral peritoneum and associated mesentery, while in Chlorophthalmus it is a discrete patch closely associated with the parietal peritoneum which lines the body cavity. In addition, larval *Parasudis* differs from larval *Chlorophthalmus* by the presence in the former of a caudad extension of pigmented mesentry (Fig. 4). Deep visceral pigmentation in other aulopiforms is discussed by Johnson (1974).

COMPARISON WITH OTHER AULOPIFORM TAXA

To assess the phylogenetic significance of certain features described in *Parasudis* we compare them here with those found in *Chlorophthalmus* and other aulopiform taxa. Clearly, the following anatomical comparisons are far from exhaustive, and we have selected only those features which appear to be phylogenetically informative at the present level of analysis.

Rosen (1971) found basihyal teeth of a similar, although larger, form and distribution in larval *Chlorophthalmus* (see also our Fig. 3C), as well as in the ipnopid larvae he described (see Okiyama 1981 for other ipnopid larvae). Sulak (1977) described comparable basihyal dentition in larval *Bathypterois,* and *Bathytyphlops.* Rosen (1971) noted that a similar basihyal dentition is unknown in any adult fish (although the pattern is approximated in *Glossanodon*). Sulak (1977:80) stated that the "...condition appears to be unique to the juvenile stages of basal myctophiform fishes." However, until the full limit of the distribution of this type of larval dentition are known, particularly in larval aulopids and neoscopelids, we can draw little phylogenetic inference from its occurrence in *Parasudis* larvae.

Basihyal morphology easily distinguishes *Chlorophthalmus* from *Parasudis,* which in *Chlorophthalmus* is short and strongly spatulate (Figs. 3A, C), and in *Parasudis* is elongate. These differences, although less markedly than in larvae, are present in the ossified adult elements and help to distinguish the taxa (compare Figs. 7B, C). Basihyal morphologies similar to those of larval *Chlorophthalmus* are found in the larvae of *Bathypterois* (Sulak 1977; personal observation) and other ipnopids (Rosen 1971; Okiyama 1981), as well as in adult *Aulopus, Bathysaurus* and *Scopelosaurus* (Bertelsen *et al.,* 1976; personal observation). Thus, based upon its limited distribution, we interpret the broad and elongate basihyal of larval *Parasudis* as an autapomorphic feature.

Interestingly, adult ipnopids share a derived condition of the basihyal element, which is relatively tiny [or entirely absent in some bathypteroids (Mead 1966)] and obliquely aligned (Fig. 7A). A similar condition of the basihyal is present in adult *Bathysauropsis,* where unfortunately the larval condition is unknown (Okiyama 1984).[2]

Certain stomiatoids have a similar basihyal arrangement, however, we agree with Weitzman (1974) that the presence of a moderately sized and horizontally aligned basihyal is primitive for the Stomiiformes as a whole. Among alepisauroids (*sensu* Rosen 1973), a small (toothed) basihyal is found in certain scopelarchid taxa (Johnson 1974) and in *Bathysaurus,* but a small vertically aligned basihyal appears to be restricted in its distribution among aulopiforms to adult *Bathysauropsis* and the Ipnopidae.[3] The common occurrence of this basihyal morphology suggests an immediate common ancestry between them.

Corroboration of the phyletic integrity of a grouping comprising *Bathysauropsis* and the ipnopids is found in the degree of development of the branchiostegal membranes and gular fold. Mead (1966:115) described the region in bathypteroids in the following

[2]We have been able to examine only two specimens of *Bathysauropsis gracilis* but have kindly been given access to notes and radiographs made by K. Sulak after his examination of specimens of *B. gigas* and *B. mayanus.*

[3]Following Johnson (1982) and Okiyama (1984) the Ipnopidae is taken here to include the Bathypteroidae of Mead (1966) and is equivalent to the Bathypteroidae of Marshall and Staiger (1975) and the sub-family Ipnopinae of Sulak (1977) and Nelson (1984).

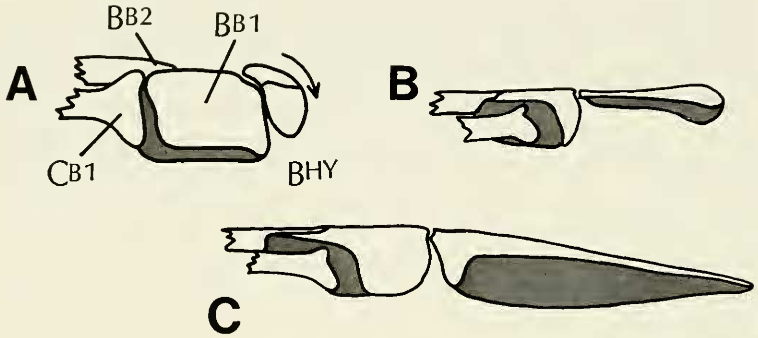

Figure 7. Basihyal and associated structures in adult (A) *Bathypterois* (MCZ 57624). (B) *Chlorophthalmus* (MCZ 41444). (C) *Parasudis* (MCZ 40561).

Abbreviations: Bb1–2, basibranchials 1–2; Bhy, basihyal; Cb1, ceratobranchial 1.

terms which apply equally to *Bathysauropsis* and the ipnopids: "Branchiostegal membranes broad and separate from one another and from the isthmus, overlapping anteriorly, and crossed near the tip of the jaw by a thick but narrow gular fold . . . " This morphology appears to be unique among aulopiforms and although a poorly developed gular fold is present in some stomiiform fishes (e.g., *Gonostoma* and *Polymetme*) it is not as elaborate as that found in *Bathysauropsis* and the ipnopids.

Chlorophthalmus shares with *Parasudis* the pigmented scale pocket skin flap character. In *Parasudis* the dorsal and ventral scale rows converge rostrad, "herringbone" fashion, upon the lateral line (Mead 1966; Fig. 47), while in *Chlorophthalmus,* dorsal and ventral scale rows diverge from the midline resulting in a slightly "zig-zag" pattern (Mead 1966; Fig. 46). This highly distinctive feature of squamation is unique to *Parasudis* and *Chlorophthalmus,* and is here interpreted as a synapomorphy uniting the two genera.

In the eyes of adult *Chlorophthalmus* (Theisen 1965; Fig. 3), as well as in adult *Parasudis,* a "keyhole" shaped aphakic space is present. Although well-developed aphakic spaces are not uncommon to the eyes of many benthic marine fishes (Munk 1966; Marshall 1971), a "keyhole" shaped space is restricted to adults of these

two genera. A similar space is absent in the eyes of *Bathysauropsis* and it is here interpreted as a synapomorphy of *Parasudis* and *Chlorophthalmus.*

RELATIONSHIPS

In reviewing the literature pertaining to *Parasudis* and its supposed relatives, it is clear that many problems remain (Johnson 1982; Rosen 1985; Stiassny 1986). However, at the intrafamilial level, aside from the suggestion that *Parasudis* may share a close phylogenetic relationship with paralepidid alepisauroids (Mead 1966), most authors who have considered the chlorophthalmids (e.g., Gosline *et al.* 1966; Marshall and Staiger 1975; Sulak 1977; Nelson 1984; Stiassny 1986) imply that *Chlorophthalmus* and *Parasudis* are closely related, and our own investigation confirms a sister-group relationship between these two taxa. The genus *Bathysauropsis* is poorly known anatomically, and consequently, its phylogenetic placement is less clear. Mead (1966) suggested that further investigation of this genus may indicate a need for familial reallocation, a finding that is corroborated by this study. We propose that the notion of an "intermediate" or "transitional" position of *Bathysauropsis,* forming a "link" between *Parasudis* and *Chlorophthalmus* on the one hand and the ipnopids on the other, and thus serving as "...the primary basis of the present incorporation of the ipnopine genera into the Chlorophthalmidae" (Sulak 1977:64) be replaced by a phylogenetic scheme in which *Bathysauropsis* is removed from the Chlorophthalmidae and incorporated within the Ipnopidae (Fig. 8). This relocation of *Bathysauropsis* is based on our observations of the presence of a small, obliquely aligned basihyal and a well-developed gular fold (Fig. 8: characters one and two). The position of *Aulopus* in relation to these taxa is here unresolved; larval aulopid material was unavailable for this study. Elsewhere Stiassny (1986) argued that *Chlorophthalmus, Parasudis* and *Aulopus* (but not *Bathysauropsis* and the other ipnopid genera) share with ctenosquamate fishes an advanced type of palatine/maxillary association and morphology (see also Rosen 1985 for a consideration of aulopid relationships). For this reason *Aulopus* is included in our cladogram, albeit in an unresolved position (Fig. 8).

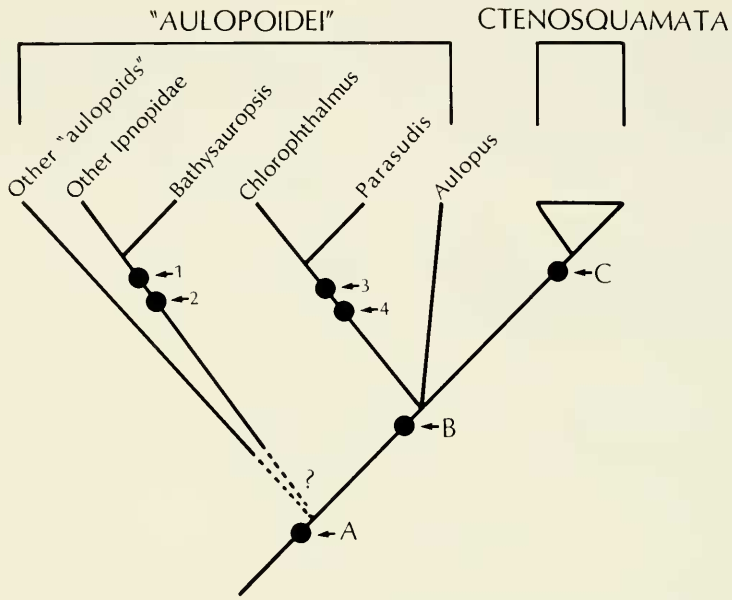

Figure 8. Cladogram of eurpterygian relationships, incorporating the results of the present study. Characters are the presence of: 1) A small obliquely aligned basihyal bone; 2) A thick well-developed gular fold; 3) A "keyhole" shaped aphakic space; 4) A peculiar scale pocket morphology and pigmentation; A) See Rosen (1985) for synapomorphies uniting the Aulopoidei with the Ctenosquamata; B) See Stiassny (1986) for synapomorphies uniting *Aulopus, Chlorophthalmus* and *Parasudis* with the Ctenosquamata; C) See Lauder and Liem (1983) for synapomorphies uniting the Ctenosquamata. Note: Following Rosen (1973), "other aulopoids" are the Bathysauridae and Notosudidae. "Other Ipnopidae" are *Bathypterois, Bathytyphlops, Bathymicrops* and *Ipnops.*

Significance of the Rostral Cartilage

Given this admittedly tentative scheme of relationships for the chlorophthalmids, it is extremely interesting to note the highly varied condition of the so-called "rostral cartilage" in these and in other aulopiform taxa. The "rostral cartilage" of both larval and adult *Parasudis* is a single median structure which is bound by a well-developed ethmo-rostroid ligament to both the ethmoid and premaxillae (Figs. 9A, B). The attachment of the cartilage to the ethmoid is strong in the larval fish and becomes weaker with growth. In

Parasudis, the rostral cartilage stains normally with Alcian Blue and is therefore presumably fully chondrified hyaline cartilage. In contrast, the "cartilage" in *Chlorophthalmus* (Figs. 9C, D; Rosen 1985; Fig. 40C) is paired, and the "cartilages" are associated with the symphyseal processes of the premaxillae. An ethmo-rostroid ligament is lacking, but the whole region is invested with loose connective tissue fibers. These rostral structures do not stain normally with Alcian Blue; staining is weak and diffuse. Similarly, in *Aulopus* (Rosen 1985; Fig. 41C; Stiassny 1986; Fig. 6) the single median structure does not stain as hyaline cartilage and is highly fibrous. Theisen (1965) illustrated paired rostral structures in *Ipnops* similar to those of *Chlorophthalmus.* Rosen (1985) also illustrated paired "rostral cartilages" of an apparently remarkably similar type and arrangement in the stomiiform, *Maurolicus.* Other stomiiform taxa examined in this study either lack a "rostral cartilage" entirely (e.g., *Photichthys*), or bear a single median structure ligamentously bound to the ethmoid region (e.g., *Gonostoma* and *Diplophos*). We have been unable to locate "rostral cartilages" in either *Bathypterois* or *Bathysauropsis.* In both of these genera the premaxillae are bound to the ethmoid region by a well-developed ethmo-rostroid ligament. We interpret the similarities between the rostral morphologies of *Chlorophthalmus* and *Ipnops* (and *Maurolicus*) to be homoplasious. To assess them otherwise, that is, to argue for the phyletic alignment of *Chlorophthalmus* with *Ipnops* (and *Maurolicus*) on the basis of this one "rostral cartilage" character would require losses and reversals in a series of other characters (see Fink and Weitzman 1982; Marshall and Staiger 1975).

Bertelsen *et al.* (1976) described and illustrated the rostral morphology of certain notosudids where a large (often ossified) "rostral cartilage" is bound to the ethmoid and the premaxillae by a well-developed ethmo-rostroid ligament similar to that of the stomiiform, *Gonostoma* (Stiassny 1986), or to that illustrated here for *Parasudis.*

Rostral morphologies are also confusing among other aulopiform lineages; for example, among synodontids, *Synodus* (Fig. 10A) bears a large medial and fully chondrified "rostral cartilage" strongly bound to the ethmoid. *Saurida* (Fig. 10B), on the other hand, lacks the structure as do both *Harpadon* and *Bathysaurus.* The paralepidid *Sudis* bears small paired hyaline cartilages, which in adults are associated with the symphyseal processes of the pre-

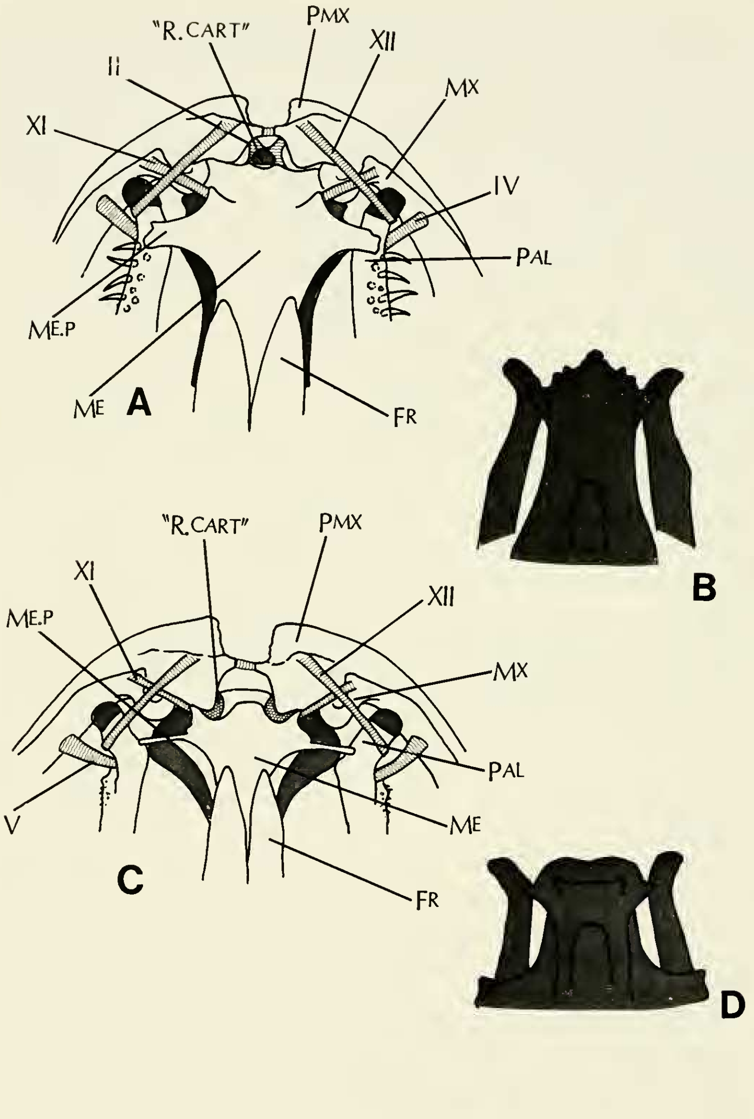

Figure 9. *Parasudis.* (A) Ethmovomer and upper jaws of adult specimen in dorsal view (MCZ 40561). (B) Ethmovomer of larva 30 mm SL (MCZ 62398) in dorsal view. *Chlorophthalmus.* (C) Ethmovomer and upper jaws of adult specimen (MCZ 40564) in dorsal view. (D) Ethmovomer of larva 22 mm SL (MCZ 62403) in dorsal view.

maxillae. In larvae these structures appear more strongly bound to the ethmoid. Finally, in *Alepisaurus* a condition much like that described in *Salmo* (Fink and Weitzman 1982; Rosen 1985) pertains. Paired hyaline cartilages are strongly bound to the inner faces of the premaxillary symphyseal processes.

Even from this cursory review it is clear the homologies of rostral morphologies and other associated structures throughout the lower Neoteleostei are questionable. By the level of the Acanthomorpha, the situation has stabilized such that there appears little doubt of the homology of the single median chondrified rostral cartilage strongly bound to the premaxillary ascending processes by a well-developed maxillo-rostroid ligament (Stiassny 1986). Until the distribution and homologies of the non-acanthomorph rostral structures are better understood, perhaps the term rostral cartilage should be restricted to that structure in the Acanthomorpha. When referring to the various rostral structures in non-acanthomorph neoteleosts before their homologies are resolved, the term "rostral cartilage" or "rostral structure" should be employed within quotation marks.

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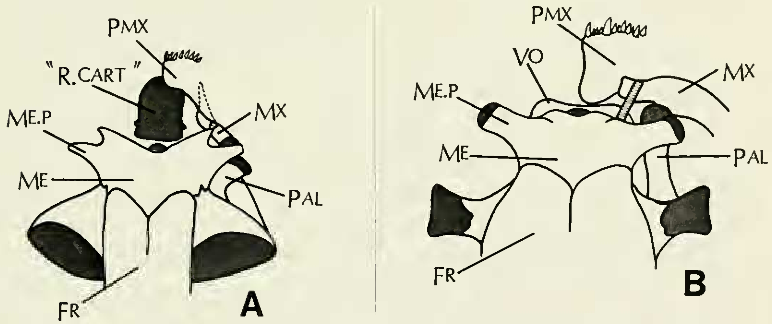

Figure 10. Ethmovomer and upper jaw of adult specimens of (A) *Synodus* (MCZ 47490). (B) *Saurida* (MCZ 56111).

Abbreviations: Fr, frontal; Me, mesethmoid; Me.p, mesethmoid process; Mx, maxilla; Pal, palatine; Pmx, premaxilla; "R.cart", "rostral cartilage". Ligaments: II, ethmo-rostroid; IV, median palato-maxillary; XI, ethmo-maxillary; XII, palato-premaxillary.

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APPENDIX

MATERIAL EXAMINED

Parasudis material

The single figure given in parenthesis after the catalogue number is SL; if more than one specimen is registered the number of specimens is given and followed by their size range.

P. truculenta

Larvae: ARC uncat. (42.8 mm), 42°27′N 58°27′W, 0–300 m, 4 Apr. 1979, USSR Belogorsk, sta. 35–4. ARC 6729 (37.3 mm), 40° 22′N 62°38′W, 0–200 m, 20 Mar. 1979. ARC 6732 (28.0 mm, c.s.), 40°

51′N 61°34′W, 0–50 m, 21 Mar. 1979. ARC 6845 (41.2 mm), 39°44′N 56°59′W, 0–200 m, 1 Apr. 1979. ARC 6879 (80.0 mm), 42°27′N 58° 27′W, 0–300 m, 4 Apr. 1979. MCZ 58531 (28.5 mm), JEC 7755, 11° 12′N 53°49′W, 60 m, 27 Mar. 1977. MCZ 62397 (38.0 mm, c.s.), JEC 7715, 0°13′N 35°44′W, 90–100 m, 15 Mar. 1977. MCZ 62398 (30.0 mm, c.s.), JEC 7750, 10°48′N 52°17′W, c.80 m, 26 Mar. 1977. MCZ 62399 (30.6 mm), JEC 7753, 10°48′N 52°17′W, c.140 m, 27 Mar. 1977. MCZ 62400 (15.4 mm), MOC 10–118, 3, 34°12′N 75°00′W, 70–0 m, 14 Aug. 1978. MCZ 63055 (40.0 mm), JEC 7737, 38°55′N 72° 25′W, 0–825 m, 3–4 Sept. 1976. MCZ 63056 (31.0 mm), JEC 7738, 38°51′N 72°27′W, 0–750m, 4 Sept. 1976. Plus an additional 32 uncatalogued MCZ specimens (11.7–49.1 mm) from the WHOI collection. USNM 258610 (20.0 mm), 31°50′N 63°56′W, 40 m, 23 Feb. 1972.

(ZMUC) DANA 1166V (11, 14.6–24.1 mm), 100 meters of wire out (mw) and DANA 1166VI (2, 14.3–21.2 mm), 50 mw, both 10° 16′N 40°41′W, 11 Nov. 1921. DANA 1168IV (41.4 mm), 300 mw, and DANA 1168VI (22, 13.8–23.9), 50 mw, both 9°30′N 42°41′W, 12 Nov. 1921. DANA 1190VIII (13.1 mm), 17°58′N 64°45′W, 100 mw, 13 Dec. 1921. DANA 11941 (10.6 mm), 17°58′N 64°41′W, 320 mw, 12 Dec. 1921. DANA 1202IV (12.5 mm), 100 mw, and DANA 1202 (11.3 mm), 50 mw, both 9°40′N 79°56′W, 10 Jan. 1922.

Transforming larvae: MCZ 57922 (75.5 mm), 11°36′N 62°46′W, 530m, 19 Apr. 1960. MCZ 62401 (85.0 mm) MOC 20–19, 0, 39°13.5′N 71°17.6′W, 0–1027m, 15 June 1982.

Adults: MCZ 39968 (9, 130–190 mm), 07°10′N 53°07′W, 360 m, 6 Nov. 1957. MCZ 40561 (22, 90–175 mm), 07°34′N 54°50′W, 360 m, 6 Nov. 1957. MCZ 40561 (3, 90–102.2 mm c.s.), 07°34′N 54°50′W, 6 Nov. 1957. MCZ 41840 (85.0 mm), 18°16′N 67°17′W, 450 m, 6 Oct. 1959. UMML 15608 (120 mm, c.s.) no data.

P. fraser-brunneri

Larvae: MCZ 62402 (31.5 mm), RHB 2053, 16°32′N 19°35′W, 50–56 m, 13 Nov. 1970.

Adults: USNM 245646 (3, 84–138), 04°26′N 08°29′W, 200 m., 31 Oct., 1963, BBC 843. MCZ 63153 (3, 97–105, one specimen c.s.), same data as USNM 245646.

Comparative material

STOMIIFORMES

Gonostomatidae—*Diplophos taenia:* MCZ 52562, MCZ uncat. c.s.; *Gonostoma elongatum:* MCZ 62404; *Gonostoma sp.:* MCZ uncat. c.s.

Sternoptychidae—*Maurolicus muelleri:* MCZ 62598, MCZ uncat. c.s.

Photichthyidae—*Photichthys argenteus:* MCZ 56953; *Polymetme corytheola:* MCZ 56968, MCZ uncat. c.s.

AULOPIFORMES

Aulopidae—*Aulopus nanae:* MCZ 40516; *A. japonicus:* MCZ 45169 c.s.

Chlorophthalmidae—*Chlorophthalmus agazzisi:* MCZ 40539, MCZ 40509 c.s., MCZ 41444 c.s.;*C. bicornis:* BMNH 1939.5.24:457; *C. brasiliensis:* MCZ 51365, MCZ 40564 c.s.; *C. chalybeius:* MCZ 62155, MCZ 40564 c.s.; *C. nigripinnis:* BMNH 1887.12.7:207; *Chlorophthalmus* sp.: MCZ 62403 c.s., MCZ 62591, MCZ 62592, MCZ 62593, MCZ 62597.

Ipnopidae—*Ipnops murrayi:* MCZ 41133; *Bathypterois phenax:* MCZ 57624; *B. quadrifilis:* MCZ 35598; *B. viridensis:* MCZ 40567 c.s.; *Bathysauropsis gracilis:* BMNH 1887.12.7:209–210.

Notosudidae—*Scopelosaurus argenteus:* MCZ 62405 c.s., MCZ 62406 c.s.; *S. harryi:* MCZ 40512.

Scopelarchidae—*Scopelarchus analis:* MCZ 62599 c.s.

Bathysauridae—*Bathysaurus agazzisi:* MCZ 55305 c.s., MCZ 62409 c.s.; *B. mollis:* MCZ 41140

Synodontidae—*Synodus synodus:* MCZ 47378, MCZ 47490 c.s.; *S. jaculum:* MCZ 46972 c.s.; *Saurida brasiliensis:* MCZ 62408 c.s.; *Sa. tumbil:* MCZ 59273; *Sa. undosquamis:* MCZ 56111 c.s.

Harpadontidae—*Harpadon* sp.: MCZ uncat. c.s.

Alepisauridae—*Alepisaurus brevirostris:* MCZ 60345, MCZ 43153 c.s.

Evermanellidae—*Evermanella* sp.: MCZ uncat. c.s.

Paralepididae—*Paralepis elongata:* MCZ 43140; *P. speciosa:* MCZ 60332 c.s.; *Lestrolepis intermedia:* MCZ 62407 c.s.; *Sudis atrox:* MCZ 60336 c.s.